



Impact of Plant Invasion and Increasing Floods on Total Soil Phosphorus and its Fractions in the Minjiang River Estuarine Wetlands, China

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Received: 20 April 2015 / Accepted: 9 October 2015 / Published online: 21 October 2015
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Abstract Plant invasion and increased flooding intensity projected by climate change models can change the soil capacity of marine wetland to store P. This is a key question to the nutrient balances and eutrophication processes of coastal areas, especially in China coastal area that is receiving the freshwaters of a country in fast economical developing process. We studied the impact of changes in flooding intensity and plant invasion on total soil-P concentrations in the Minjiang River estuarine wetland. Flooding had a weak positive effect on soil P-fractions concentrations, but this effect was largely counteracted by the negative effect of salinity. Soil clay concentration and pH, both of which were related more with species community composition than with flooding intensity, were directly related to the P-fraction concentrations. The replacement of the native mangrove community by the invasive plant *Phragmites australis* was related to a decrease in the soil capacity to store P. A suitable management to maintain

this wetland area in optimum conditions to act as a natural eutrophication buffer should tend to favor mangrove communities in the new areas that reach more than 220 days y⁻¹ of flooding, and a combination of the three tall-grasses communities below this level of flooding.

Keywords Clay · Flooding · Invasive plants · *Cyperus malaccensis* · Mangrove · *Phragmites australis* · N:P · Soil P · Soil P fractions · Soil pH · Soil texture · *Scirpus triqueter*

Introduction

Phosphorus (P) is a crucial element for all living organisms. Next to nitrogen (N), P is the nutrient that most commonly limits plant production in the terrestrial biosphere (Margalef 1997; Aerts and Chapin 2000). Several drivers of global change such as N eutrophication, changes in soil use, species invasion or climate change currently have serious impacts on the P cycle and P imbalances and other important bioelemental cycles, such as that of N (Sardans et al. 2006; Peñuelas et al. 2012 and 2013). The question now arises whether or not P and its imbalances with other nutrients can alter the capacity of Earth to fix C from anthropogenic emissions of carbon dioxide (Peñuelas et al. 2013).

Global warming is affecting ocean levels through its impacts on the global water cycle (Schewe et al. 2011; Mendelsohn et al. 2012; Piecuch and Ponte 2014), and nutrient stoichiometry (Sardans et al. 2012a; Sardans and Peñuelas 2014a, b). These effects of global warming can further affect the global P cycle and its stoichiometric relationships with other nutrients, which can then affect community structure and function (Sturner and Elser 2002; Sardans et al. 2012b; Peñuelas et al. 2012 and 2013).

Electronic supplementary material The online version of this article (doi:10.1007/s13157-015-0712-9) contains supplementary material, which is available to authorized users.

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The increase in ocean levels could be especially critical for wetland ecosystems (Ramsar 2013). Flooding in these important ecosystems can alter soil contents and the stoichiometric relationships of C, N, P, and sulfur (S) by changing the aerobic/anaerobic biogeochemical equilibrium, nutrient inputs and outputs, and/or the structures of plant communities (Steinman et al. 2012; Recha et al. 2013; Wang et al. 2013), and by altering water flow and fluxes (Zak et al. 2008; McCray et al. 2012). Wetlands are also frequently affected by other drivers of global change such as species invasions that can interact with the increase in flooding duration and intensity to change the capacity of wetlands to store P and/or to change the proportions of different soil-P fractions. Moreover, the expected increase of typhoon events will increase the flood time, water table, soil salinity and anoxic conditions. Furthermore, typhoon events increase litterfall and nutrient cycling in plant-soil system (Wang et al. 2015c).

Estuaries and marshes are sinks for the wastewater from human activities that frequently contain high concentrations of P loaded to rivers (Mustafa and Scholz 2011; Wang et al. 2012). Despite the high priority at a global scale of wetland restoration (Mustafa and Scholz 2011; Dunne et al. 2011; Zak et al. 2014), wetlands restored on former agricultural land could potentially release accumulated P and become a source of eutrophication (Kjaergaard et al. 2012; Kinsman-Costello et al. 2014). Under increasing intensities of flooding, we should expect higher levels of anoxic conditions, under which increased Fe^{3+} reduction could increase the release of P from Fe^{3+} phosphates (Zak et al. 2008; Kjaergaard et al. 2012).

Invasions of alien plant species are currently increasing and are a serious threat to global plant diversity (Vitousek et al. 1987; Funk and Vitousek 2007). Most studies that have investigated alien success have identified nutrient availability and the competitive capacities of nutrient uptake and of coping with low levels of nutrients as the key factors accounting for the success of the alien species (Sardans and Peñuelas 2012a, 2012b; Drenovsky et al. 2012). Moreover, alien plants frequently alter soil nutrient concentrations and availability, the decomposition of organic matter, nutrient cycling, and soil stoichiometry (Sardans and Peñuelas 2012a, 2012b; Drenovsky et al. 2012). Invasive plant species, such as the common reed, *Phragmites australis*, are spreading in several Chinese wetlands (Tong et al. 2011; Wang et al. 2015a). The success of *P. australis* has been associated with its higher nutrient-use efficiency and up-take capacity than native species (Wang et al. 2015a). We hypothesized that increased flooding could have an impact on its invasive success and its interactions with plant-soil P-cycle, which in turn could affect the effect of flooding intensity on the status of soil P in wetlands.

China coastal areas receive great amounts of P (Sharpley and Wang 2014; Gao et al. 2015; Li et al. 2015), that have increased by a factor of 2–5 in the period 1970–2000 and threaten to increase additional 30–200 % towards 2050 (Stokal et al. 2014). We hypothesized that total P and P-fractions in soil will change in function of flooding intensity and plant community, and therefore the increase or decrease of wetlands capacity to act as a P sink or source in the next decades can be projected in an scenario of flooding enhancement and reduction of wetland surface and enlighten the management possibilities of improving such capacity.

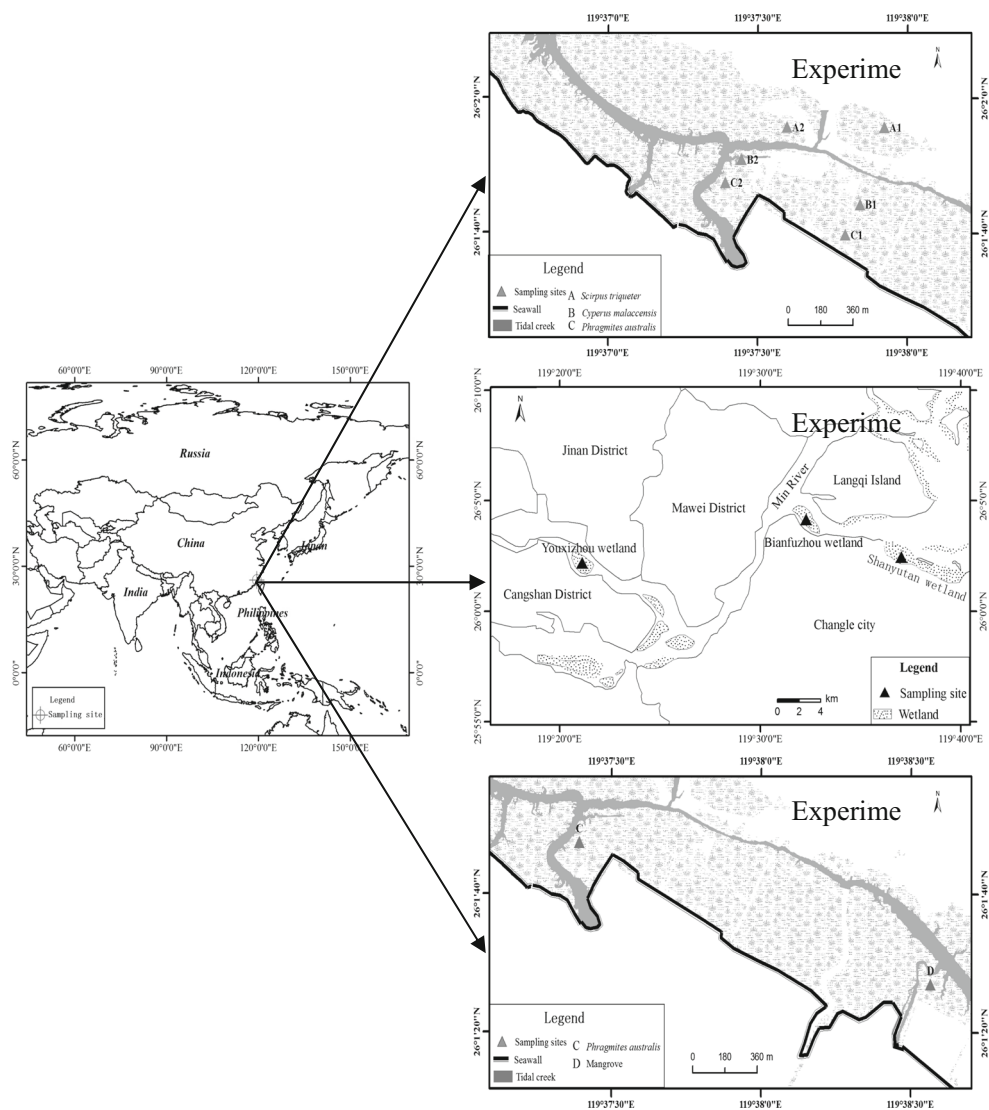
We studied soil-P concentrations under different flooding gradients and under the absence/presence of an invasive species in the Minjiang River estuarine tidal wetland to clarify their effects on P concentrations and fraction variations. We aimed to answer the questions: (i) how do increased flooding and different plant communities, including a successful invasive plant species, affect the concentrations and contents of total soil P and the soil P fractions, and (ii) which physico-chemical soil properties are involved in these effects?

Material and Methods

Study Areas

This study was conducted in the Minjiang River estuarine wetland in southeastern China, in the transition zone of the mid-subtropical and south subtropical zones (25°50'43"-26°9'42"N, 119°5'36"-119°41'5"E). The estuary has an area of 476 km² and a relatively warm and wet climate, with a mean annual temperature of 19.7 °C and a mean annual precipitation of 1346 mm (Liu et al. 2006). Many wetlands are distributed in the estuary and along the river. We conducted three experiments in this study (Fig. 1).

- (1) *P. australis* and the native sedges *Scirpus triquetus* L. and *Cyperus malaccensis* var. *brevifolius* Boeckeler are the plant species that dominate the land surface in the Shanyutan wetland and are typically found in the upper (mid to high) portions of mudflats (Liu et al. 2006). These three species can grow in both high-flood and low-flood habitats. We established an experimental setup in this wetland at two flooding intensities and with three species communities. The flooding in the studied areas is based on the tide flood, and therefore depends on the distance to sea. Changes in river flow are also important to control the flood, but the main responsible of the differences of flooding intensity across different wetland areas is sea tidal. The high-flood habitats are flooded by intermediate tides ca. 240 d y⁻¹ and are submerged beneath 10–120 cm of water for 0.5–4 h during each tidal inundation. The areas occupied by each species were ca.

Fig. 1 Location of the the sampling sites

8, 9, and 18 hm^2 for *S. triquetar*, *C. malaccensis*, and *P. australis*, respectively. The low-flood habitats are flooded only during spring tides, ca. 80 d y^{-1} , and are submerged beneath 10–50 cm of water for 0.5–2 h during each tidal inundation. The areas occupied by each species were ca. 7, 12, and 6 hm^2 for *S. triquetar*, *C. malaccensis*, and *P. australis*, respectively. The soil surfaces of both the low- and high-flood habitats of the entire estuarine wetland are exposed at low tide, but the soil remains flooded in some low areas. We analyzed two flooding intensities \times three communities \times six soil layers \times three replicates, for a total of 108 samples. With this experiment we analyzed how different flood intensities are related with differences in soil P concentrations and P-fraction in soils under each one of the three tall-grasses depending on flooding intensity.

- (2) Communities of the invasive *P. australis* in the Shanyutan, Bianfuzhou, and Youxizhou wetlands were selected as

high-flood, intermediate-flood, and low-flood habitats, respectively, from the coast inland to test the effects of flooding intensity on the total soil-P concentration and content and different P fractions. The high-flood habitat (Shanyutan wetland) is flooded by tides ca. 240 d y^{-1} and is submerged beneath 10–120 cm of water for 0.5–4 h during each tidal inundation. The intermediate-flood habitat (Bianfuzhou wetland) is flooded by tides ca. 220 d y^{-1} and is submerged beneath 10–100 cm of water for 0.5–3 h during each tidal inundation. The low-flood habitat (Youxizhou wetland) is flooded by tides ca. 180 d y^{-1} and is submerged beneath 10–70 cm of water for 0.5–1.5 h during each tidal inundation. We analyzed three flood intensities (the high-flood intensity was the same as that in the first experiment for *P. australis*) \times one community \times six soil layers \times three replicates, for a total of 54 samples (36 were different from those in the first experiment). With this

study we analyzed whether or not soils under the invasive species *P. australis* have different P and P-fractions concentrations at different levels of flooding intensity.

- (3) *P. australis* in the Shanyutan wetland subjected to high-flood intensity has invaded the wetland over the past 30 years and is now the most prevalent plant species occupying the natural habitat of the native mangroves. *P. australis* has spread occupying sites that previously were covered by mangrove communities. Mangroves had not a high density, and humans tend to reduce its density and to allow *P. australis* spreading. We investigated and compared total soil-P concentration and content and different P fractions in the *P. australis* communities and in the natural mangrove habitat in this high-flood habitat. We analyzed one flooding intensity (high) × two communities (the data for *P. australis* were the same as for the high-flood intensity in the first experiment) × six soil layers × three replicates, for a total of 36 samples (18 were different from those in the first experiment). With this experiment we analyzed the differences in P and P-fractions concentrations between the invasive *P. australis* tall-grass and the native mangrove community in the current wetland areas submitted to the high levels of flooding intensity.

Collection and Analysis of Soil Samples

Soil samples were collected in October 2007 from the *S. triquetra*, *P. australis*, *C. malaccensis*, and mangrove communities in the high- and low-flood habitats. Three replicate plots were randomly established in each community at each flooding intensity. Soil profiles (width, 1 m; length, 1 m; depth, 0.6 m) were excavated, and samples were collected with a small sampler (length, 0.3 m; diameter, 0.1 m) from each of six soil layers (0–10, 10–20, 20–30, 30–40, 40–50, and 50–60 cm) at the centers and both sides of the soil pits. These three samples were bulked to form one sample per layer. A total of 162 soil samples were thus collected (108 for the first experiment plus an additional 36 and 18 samples for the second and third experiments, respectively). In the laboratory, the samples were air-dried, roots and visible plant remains were removed, and the soil was finely ground in a ball mill.

Soil P Analyses

Total P (TP) and total inorganic P (Pi) concentrations were determined following the method described by Ruban et al. (1999) (see Appendix 1 in Supplementary Information for details).

Total organic P (Po) concentrations were determined by rinsing the residual soil in the above centrifuge tubes twice

with 12 ml of deionized water, freeze-drying, ultrasonicing in a bath for 30 s, ashing for 3 h at 450 °C, transferring to 100-ml centrifuge tubes after cooling, adding 20 ml of 3.5 mol L⁻¹ HCl, mixing on the QHZ-98A oscillator at 250 rpm for 16 h at 25 °C, and then centrifuging at 2000 g for 15 min. The P concentrations of the supernatants were determined colorimetrically as for Pi.

We used the continuous extraction procedure of Lu (1999) to determine the P concentrations in the labile Po, moderately labile Po, moderately resistant Po, and highly resistant Po fractions (see Appendix 1 in Supplementary Information for details). We used the continuous extraction procedure of Ruban et al. (1999) to determine the P concentrations in the exchangeable Pi, Fe ± Al Pi, and Ca Pi fractions.

Residual Pi P concentration was determined by:

$$[\text{residual Pi}] = [\text{TP}] - [\text{exchangeable Pi}] - [\text{Fe} + \text{Al Pi}] - [\text{Ca Pi}] - [\text{total Po}].$$

Determination of Other Soil Parameters

Total S concentrations were determined by method of Lu (1999) (see Appendix 1 in Supplementary Information for details).

Soil bulk density was measured from three 5 × 3 cm cores per soil layer (Wang et al. 2014), salinity was measured with a DDS-307 conductivity meter (Boqu Scientific Instruments, Shanghai, China), pH was measured with an 868 pH meter (Orion Scientific Instruments, USA), soil particle-size (clay, silt, and sand) contents were determined with a SEDIMAT4-12 particle size analyzer (UGT Scientific Instruments, Müncheberg, Germany), and soil-water content was determined gravimetrically (Lu 1999).

Determination of Soil C, N, and P Storage

The C, N, and P storages for all soil layers were estimated by following Mishra et al. (2010):

$$C_s = \sum_{j=1}^n c_m \times \rho_b \times D$$

where C_s is C, N, or P storage (kg m⁻²), j is the soil-depth interval (1, 2, ... n; 0–10, 10–20, 20–30, 30–40, 40–50, and 50–60 cm) c_m is the C, N, or P concentration (g kg⁻¹), ρ_b is the bulk density (kg m⁻³), D is the thickness of each soil layer (m), and n is the number of soil layers.

Statistical Analyses

The statistical significance of differences in the soil parameters among the flooding intensities and soil layers in the communities was assessed with general linear models and Tukey's

post-hoc tests. We determined the Pearson correlation coefficients among all pairwise soil studied parameters. We also determined the effects of water content and species on N and P storage. All univariate statistical analyses were performed using SPSS 13.0 (SPSS Inc., Chicago, USA).

We performed multivariate discriminant function analysis (DFA) to determine the importance of total C, N, P, and S concentrations; DOC, NH_4^+ , NO_3^- , and available-S concentrations; exchangeable Pi, Fe + Al Pi, Ca Pi, residual Pi, labile Po, moderately labile Po, moderately resistant Po, and highly resistant Po concentrations; exchangeable Pi:labile Po and total Pi/Po ratios; and total C:N, C:P, N:P, C:S, N:S, and P:S ratios in the separation of the chemical components of the soil in the plots at different flooding intensities for the three species (Raamsdonk et al. 2001). The DFAs were performed using Statistica 6.0 (StatSoft, Inc., Tulsa, USA). All nutrient ratios were calculated in mass basis.

We performed structural equation modelling to determine the best model for explaining the TP concentration, exchangeable Pi concentration, the exchangeable Pi:labile Po ratio, the total Pi:Po ratio, and the recalcitrant P concentration (endogenous variables) as functions of the flooding intensity (as a dummy variable), and the other soil traits such as soil salinity, pH and clay concentrations (exogenous variables). This analysis provided information for the direct, indirect and total effects of the exogenous variables on the endogenous variables and allowed us to determine the direct and indirect relationships of exogenous variables on endogenous variables. For example the direct effect of flooding intensity on total soil P concentrations can be distinguished from the indirect effect of flooding on total soil P due to the effect of flooding intensity on salinity that thereafter has an effect on soil total P concentration. We fitted the models using the sem R package (Fox et al. 2013) and achieved the minimum adequate model using the Akaike information criterion (AIC). Standard errors of the effects were extracted by bootstrapping (1200 repetitions) (Davison et al. 1986; Mitchell-Olds 1986).

Results

Effects of Flooding, Soil Physicochemical Traits and Species on Soil-P Pools (Experiment 1)

Flooding increased soil P concentrations of all studied Pi and Po fractions in the *S. triquetra* community but not in soils under the communities dominated by the other two species: the other native species, *C. malaccensis* and the invasive species *P. australis* that did not change P concentrations under higher flooding duration (Fig. 2, Table S1). The results of the repeated measures ANOVA (in space) are very similar to those of the GLM analysis of the flooding effect on the variables shown in Fig. 2 (Table S1). In the GLM analyses with

flooding duration, species and soil depth as independent categorical variables, only the Fe + Al P pools differed, with the Fe + Al Pi pool being higher and the Fe + Al Po (moderately labile) pool lower for *C. malaccensis* than for *P. australis* (Table S2). This asymmetrical effect of increased flooding dependent on species is clearly shown by the PCA with all soil variables, where the PC1 scores for the *S. triquetra* soils subjected to low flooding are very different than those for all other soils (Fig. 3). The PCA indicated that bulk density, sand content, and the total Pi:Po ratio were higher in the *S. triquetra* soils subjected to low flooding (Fig. 3).

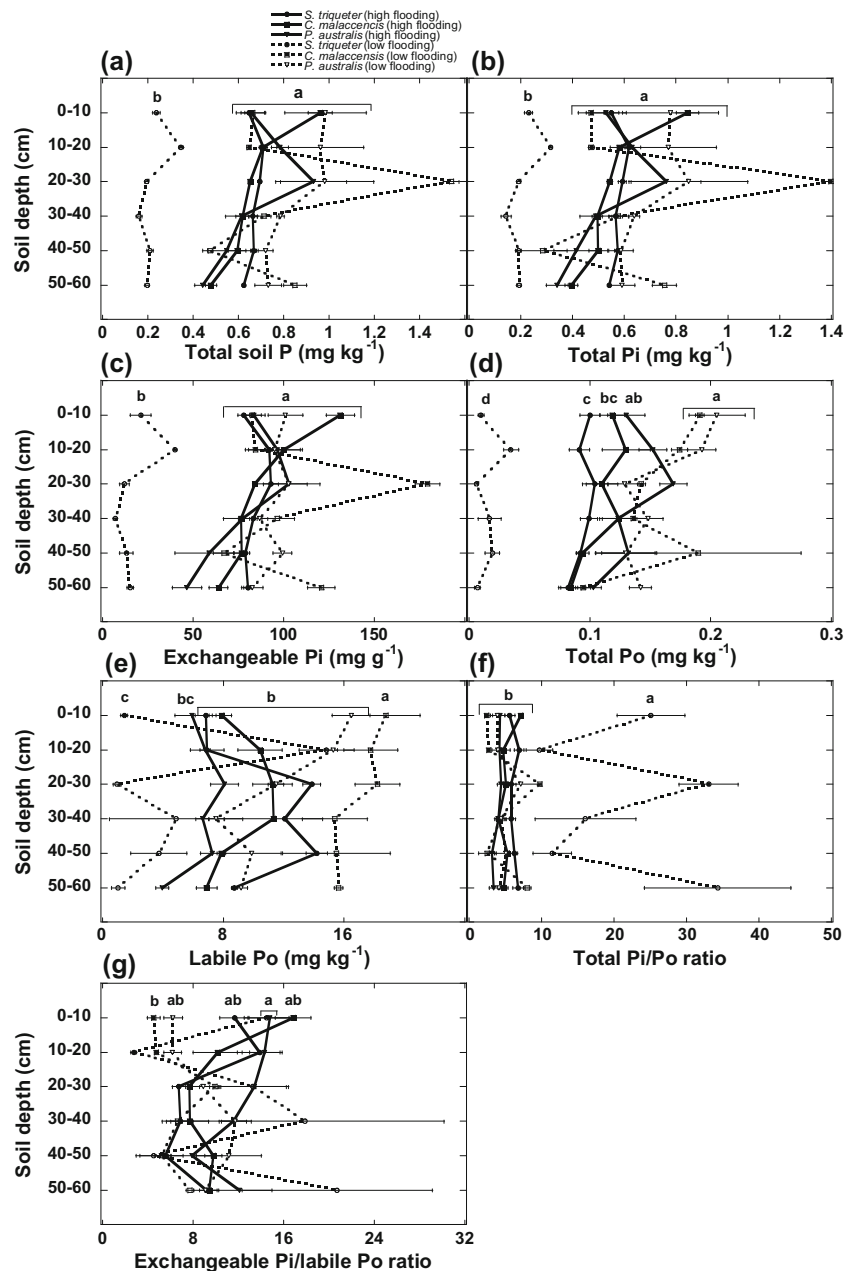
Bulk density was lower (higher silt and lower sand contents) under high flooding intensity, and soil-water content, salinity, and C and N concentrations were higher (Table S2). We observed a significant interaction flooding intensity x species, due to that these effects were particularly observed for *S. triquetra* soils and much less in the other two species. Higher NH_4^+ and lower NO_3^- concentrations were found at high flooding than at lower flooding intensities (Table S2). TP concentration and the concentrations of most P pools were positively correlated with clay and silt contents, total C and N concentrations, DOC concentration, and NO_3^- concentrations and negatively correlated with sand content, bulk density, and S concentration (Table S3). These correlations were stronger in Pi fractions than in Po fractions. Consequently, clay and silt contents and total C, N, and DOC concentrations were negatively correlated with the total Pi/Po ratio, and sand content and bulk density were positively correlated with the total Pi:Po ratio (Figure S1). These effects were mainly due to the large differences between the *S. triquetra* soil under low flooding intensity and all other soils (Figure S1).

The total N:P ratios were higher under flooding in the wetlands of the three species at most soil depths (Table S2, Fig. 4). Moreover, this ratio was highest for the invasive *P. australis* soils (Table S2, Fig. 4).

The structural models that best explained (lower AIC) the different P fractions and their Pi:Po ratios are shown in Figs. 5, 6 and 7. The best model for TP and exchangeable Pi (Fig. 5) concentrations showed that clay content and soil pH had direct positive significant effects on these P variables and that flooding had an indirect negative effect through its positive effect on salinity that subsequently had a negative effect on these P variables (Figs. 5, 6 and 7).

The best structural model for total recalcitrant P (Pi + Po) and total Po concentrations indicated a direct effect of clay content but not of soil pH, while an indirect effect of flooding by increasing salinity was also observed (Figs. 6 and 7). This relationship is consistent with the expected according to clay properties. The indirect negative effect of flooding on the exchangeable Pi:labile Po ratio was best explained by the direct effect of flooding on higher total S concentrations that subsequently had a negative effect on the exchangeable Pi:labile Po ratio (Fig. 7).

Fig. 2 Distribution of soil P variables (mean \pm SE, $n = 3$) in the soil profiles of the wetlands dominated by *S. triquetra*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities



Soil pH and mainly clay content thus had strong positive relationships with P-fraction concentrations, and these effects were stronger in the Po than the Pi fractions, and both consequently decreased the total and exchangeable Pi:labile Po ratios (Figs. 5 and 7). Flooding had no significant direct effects on clay content or soil pH. These results were consistent with those of previous univariate analyses where the variability of clay content and soil pH were slightly related with flooding intensity when comparing overall soils. The relationships between clay content and soil pH with flooding intensity were positive in soils under *S. triquetra* and negative in soils under the other two species (Fig. 8).

Effects of Flooding on the Soil-P Pools in the Invasive *P. australis* Communities (Experiment 2)

The *P. australis* soil in the mid-flood habitat had the highest TP concentrations and stored more P, mainly in the upper 30 cm of the soil, relative to the low- and high-flood habitats (Fig. 9a and 9l), due mainly to the high concentrations of the Pi pools (Fig. 9 b-e). The exchangeable Pi:total P ratio in the upper 30 cm of soil were higher in the mid- than the low- and high-flood habitats dominated by this invasive species (Fig. 9m). The PCA with all soil variables indicated that PC1 (explaining 44.7 % of the total variance) significantly ($P < 0.05$) separated

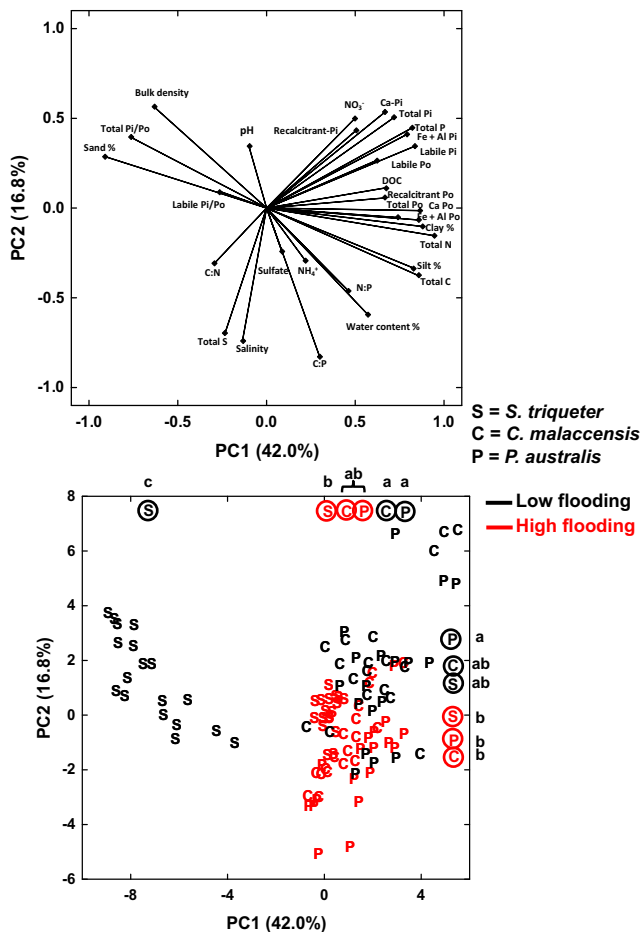


Fig. 3 Distribution of variables and cases in the plot of the first two PCs of the PCA analysis conducted with the P fractions and other soil variables in the wetlands dominated by *S. triquetra*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities

the scores of the stands of *P. australis* growing under the three flooding intensities. The concentrations of the Po pools increased from soils under low flooding to soils under high flooding intensities, coinciding with a decrease in sand content and bulk density and with an increase in clay and silt contents (Fig. 10). Interestingly, the PC2 scores (explaining 27.2 % of the total variance) for the soils in the mid-flood habitat differed significantly from the scores for the soils in the low- and high-flood habitats ($P = 0.004$ and $P = 0.0001$, respectively) (Fig. 10). PC2 was significantly loaded by TP concentration, total P stored in the soil, and all Pi pools, with the soil in the mid-flood habitat placed toward the highest values and coinciding with lower C:P ratios (Fig. 10). Increased flooding was associated with an increase in total N:P ratios (Fig. 11).

Differences in Soil P Contents Between Mangrove and Communities Dominated by the Invasive *P. australis* (Experiment 3)

Mangrove soils accumulated more P in the upper 10 cm of the soil than the *P. australis* soil at the same flooding intensity

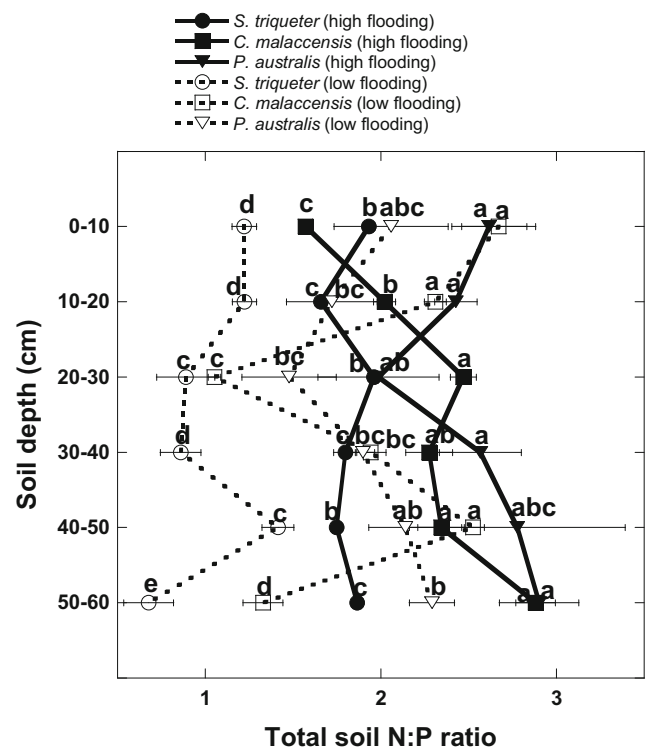


Fig. 4 Distribution of total N:P ratio (mean \pm SE, $n = 3$) in the soil profiles of the wetlands dominated by *S. triquetra*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities

(Fig. 12). The mangrove soils had higher bulk densities, sand contents, pHs, salinities, and NO_3^- concentrations and lower water contents, silt contents, total C and N concentrations, and total N:P ratios than the *P. australis* soils (Table S4). The P stored in the upper 60 cm of soil were marginally significantly ($P = 0.08$) higher in the mangrove soils than the *P. australis* soils (Table S4).

The PCA with all soil variables indicated that the scores of the mangrove soils were significantly ($P < 0.0001$) separated from those of the *P. australis* soils along the PC1 axis (explaining 31.2 % of the total variance) (Fig. 13). This axis was significantly loaded by sand content, bulk density, pH, salinity, P storage, water content, and NH_4^+ concentration, with the mangrove scores placed toward higher pH, P storage, sand content, bulk density, and salinity and toward lower water content and NH_4^+ concentration (Fig. 13).

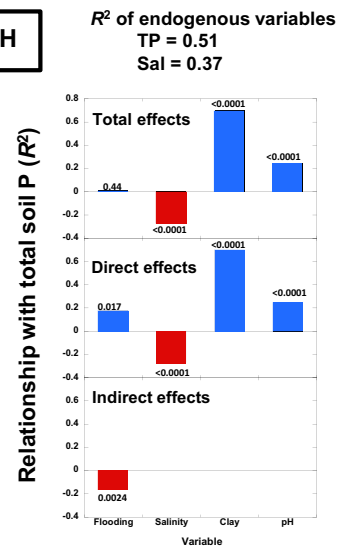
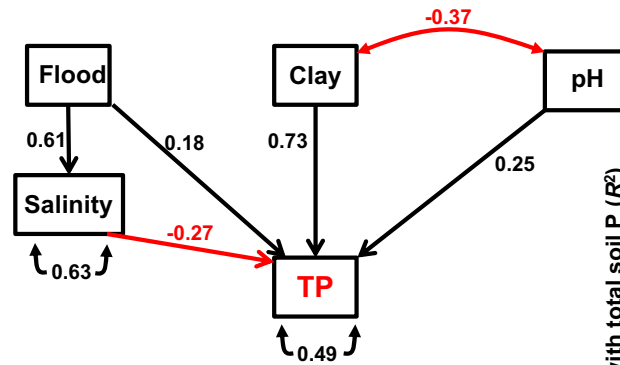
Discussion

Flooding Effects Versus Species Effects on the Status of Soil P

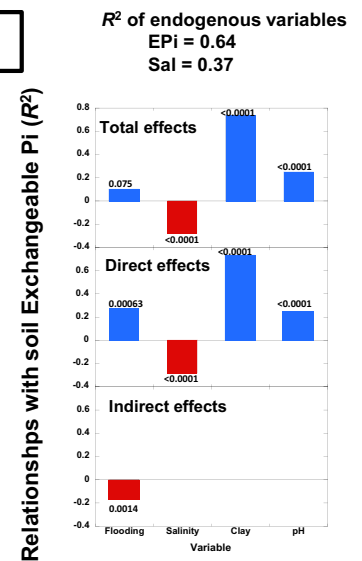
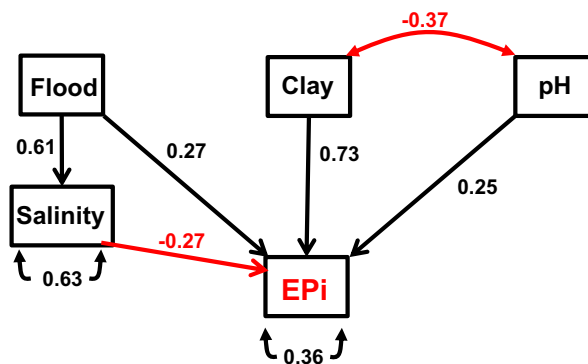
The relationships of flooding and the P pools were very asymmetrical, depending on the species. Despite we did not can disentangle if differences in soils P concentrations in soils under the different species were the cause or the effect of the

Fig. 5 Diagrams of the structural models that, by using different physicochemical soil variables and flooding intensity, best explain the variability of total soil P (TP) concentrations and total exchangeable inorganic P (EPI) concentrations in the soil profiles of the wetlands dominated by *S. triqueter*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities. The total, direct, and indirect effects of each exogenous variable on the endogenous (TP and EPI) variables are shown in each case with the level of significance (*P* value). *Black arrows* in the diagram mean positive relationships and *red arrows* negative relationships. The *bar figures* show the total direct and indirect relationships of physicochemical soil variables and flooding intensity with total soil P and exchangeable inorganic P (EPI) concentrations

Total soil phosphorus concentration (TP)



Soil labile inorganic phosphorus (EPI)



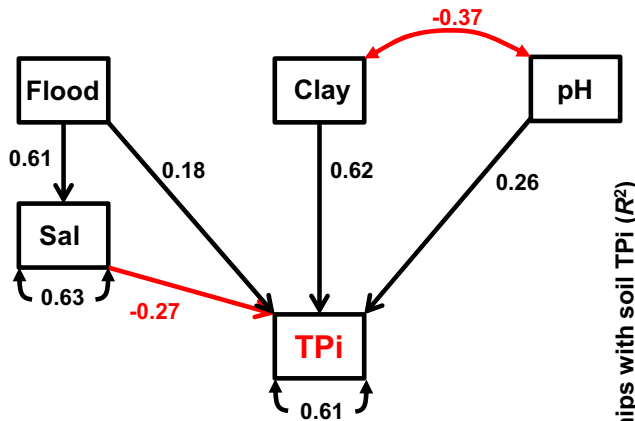
presence of these species, the P pools changed most in the soils depending on the flooding intensity in the native *S. triqueter* wetlands than in the sites dominated by the other two studied species. These differences may be related, at least partially, to the very much lower biomass of the *S. triqueter* community than those of the *C. malaccensis* and *P. australis* communities (Wang et al. 2015b). The TP concentrations of ca. 0.7 g kg⁻¹ in the first few centimeters of soil in these wetlands were within the range of 0.3–1.3 g kg⁻¹ observed in marine and estuarine wetland areas around the world (Carol et al. 2012; Xu et al. 2012; Irick et al. 2013; Gao et al. 2014; Yu et al. 2014). The concentrations of most P

fractions abruptly decreased at a depth of 30 cm. Most of the P was stored in the first few centimeters of the soil profiles, as in other wetland areas (Wang et al. 2011; Gao et al. 2014). These areas are thus very vulnerable to P losses from any disturbance that could pose a potential risk of an increase in P in the water column, and consequently its potential export to coastal areas.

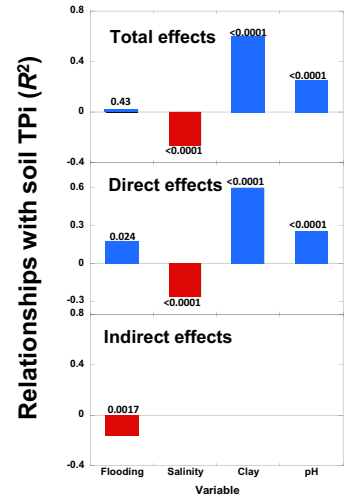
Flooding increased TP accumulation, several P fractions, and the exchangeable Pi:labile Po ratio, but these effects were partially counteracted by the indirect effects of flooding on soil salinity and total S concentration, because these variables had negative effects. Clay content and soil pH, however, were

Fig. 6 Diagrams of the structural models that, by using different physicochemical soil variables and flooding intensity, best explain the variability of total soil inorganic P (TPi) concentrations and total organic P (TPo) concentrations in the soil profiles of the wetlands dominated by *S. triqueter*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities. The total, direct, and indirect effects of each exogenous variable on the endogenous (TPi and TPo) variables are shown in each case with the level of significance (*P* value). *Black arrows* in the diagram mean positive relationships and *red arrows* negative relationships. The *bar figures* show the total direct and indirect relationships of physicochemical soil variables and flooding intensity with total soil inorganic P (TPi) concentrations and total organic P (TPo) concentrations

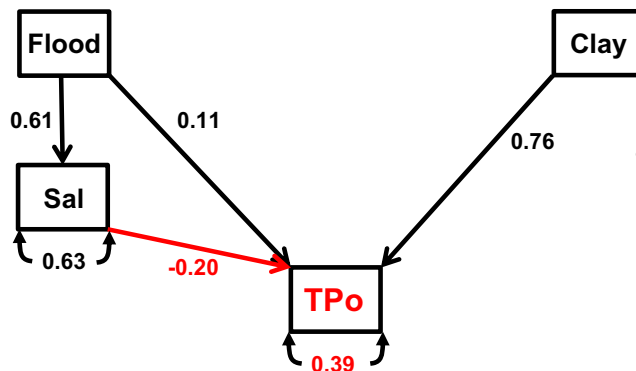
Total soil inorganic phosphorus concentration (TPi)



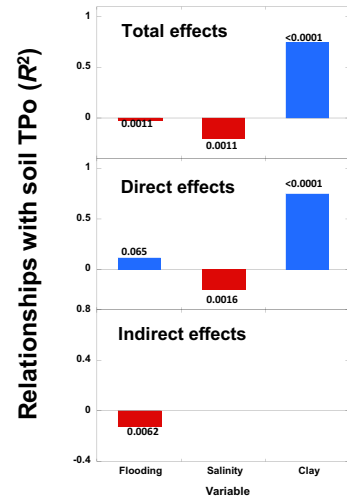
R² of endogenous variables
 TPi = 0.39
 Sal = 0.37



Total soil organic phosphorus concentration (TPo)



R² of endogenous variables
 TPo = 0.61
 Sal = 0.37



mostly associated with the various soil P fractions concentrations that in turn were more related with the dominant species and with the interaction between species and flooding than with flooding intensity alone. Most of the variability of the P concentrations was explained by the variation of the clay contents of the *S. triqueter* communities, which were lowest under lower flooding intensity, along with the lowest concentrations of all P fractions and especially the Po fractions. Higher clay contents were associated with higher sulfur concentrations (under high redox potential of the media) and lower soil pHs, consistent with the higher

anoxic conditions expected in soils with high clay contents (Miller et al. 2001; Oxmann et al. 2009). The unique important and general effect of flooding intensity on the P fractions was due to its effect on soil salinity. Pore-water salinity in wetlands has been associated with flooding intensity and thus with species composition and P concentration (Mendoza et al. 2012). These associations may be due to the effects of soil salinity on plant P uptake and thus on the P concentrations and contents in the leaves and litter, together decreasing the capacity of P retention in the ecosystem with increasing salinity (Mendoza et al. 2012).

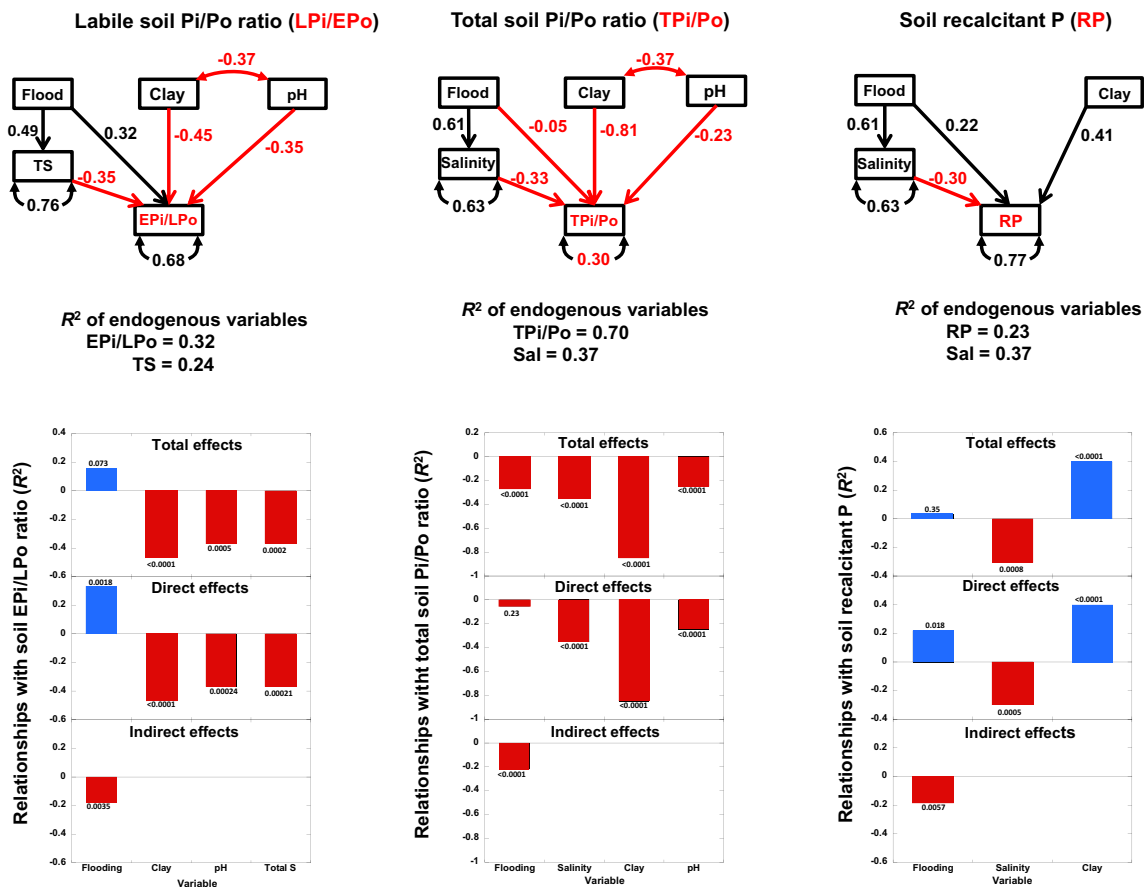


Fig. 7 Diagrams of the structural models that, by using different physicochemical soil variables and flooding intensity, best explain the variability of exchangeable-Pi:Labile-Po ratio (EPI:LPO), total Pi:Po ratio (TPI:Po), and soil recalcitrant P (RP) concentrations in the soil profiles of the wetlands dominated by *S. triquetra*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities. The total, direct, and indirect effects of each exogenous variable on the

endogenous (EPI:LPO, TPI:Po, and RP) variables are shown in each case with the level of significance (P value). *Black arrows* in the diagram mean positive relationships and *red arrows* negative relationships. The *bar figures* show the total direct and indirect relationships of physicochemical soil variables and flooding intensity with exchangeable-Pi:Labile-Po ratio (EPI:LPO), total Pi:Po ratio (TPI:Po), and soil recalcitrant P (RP) concentrations

In our studied sites, settling rates depend partially of the number of hours of flooding. Thus the longer times that water covers the soil as flooding intensity increases should permit higher particle sedimentation, which should be more relevant for clay particles than for the larger sand particles. Moreover, higher clay contents and anoxic conditions should produce lower pHs. But higher flooding intensity was associated with higher clay contents, within the range of flooding intensities of this study only in the wetlands dominated by *S. triquetra*. Our results, thus, suggested that soil clay content could be related with the specific-species cover at some extent. Anyway, the study design was not aimed to disentangle whether the high clay soil concentrations under *S. triquetra* in specially at high flooding intensity is a cause of the occurrence of this species in rich-clay soils or they are the consequence of the existence of this species increasing the capacity to trap clay particle. In another study, exchangeable Pi increased and labile Po decreased under flooding (Newman and Pietro 2001).

The clay concentrations were negatively correlated with the total ($R^2 = 0.44$, $P < 0.00001$) and exchangeable Pi:labile Po ratios ($R^2 = 0.22$, $P < 0.00001$), suggesting that Po mineralization was hindered by high clay contents. Clay content was also negatively correlated with soil pH, but this relationship was not associated with flooding intensity; soil pH was thus not clearly associated with flooding. In contrast to the expected decrease in pH with the more anoxic soil conditions under higher flooding intensity, some studies have observed that soil pH increased with flooding intensity (Saint-Laurent et al. 2014).

Previous studies in wetlands have also reported relationships between clay content and P storage (Chapuis-Lardy et al. 2006; McGrody et al. 2008; Wang et al. 2013), due mostly to high Fe-Al P and Ca P fractions and to the higher adsorption capacity of the soil, because high clay contents provide more solid and large surface per unit weight (Wang et al. 2013). In fact, and consistent with these observations, the Fe + Al Po fraction was the fraction best correlated with clay

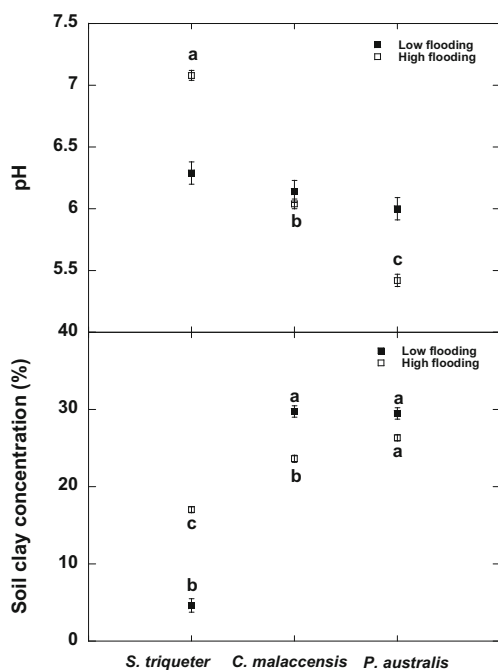


Fig. 8 pH and clay contents (mean \pm SE, $n = 3$) in the soil profiles (0–60 cm) of the wetlands dominated by *S. triquetra*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities

content ($R^2 = 0.62$). Our results thus demonstrate that these effects were mainly related to the species, despite the effects of flooding intensity on the P fractions in the soil profile. Xu et al. (2012) have also suggested that the vegetation could significantly influence P dynamics and availability in the Yellow River delta. However, we can not disentangle whether the different soil texture under the different studied species-communities is the cause or the effect of these species distribution.

The concentrations of TP and in the P fractions mostly did not differ significantly between the *P. australis* and *C. malaccensis* soils. We only observed differences in the Fe + Al P fractions, with higher Fe + Al Pi and lower Fe + Al Po concentrations in the *C. malaccensis* soils, consistent with the slightly higher rates of litter mineralization observed in *C. malaccensis* soils than in *P. australis* soils (Tong et al. 2011). The lack of general differences in the status of soil P between these two species was consistent with the small differences in litter elemental composition in the same wetlands (Tong et al. 2011). But despite the little differences observed in litter composition, we have observed some stoichiometrical differences between these two species in litter C:P (555 ± 1 and 473 ± 1 , $P < 0.0001$, respectively) and N:P (12.8 ± 0.04

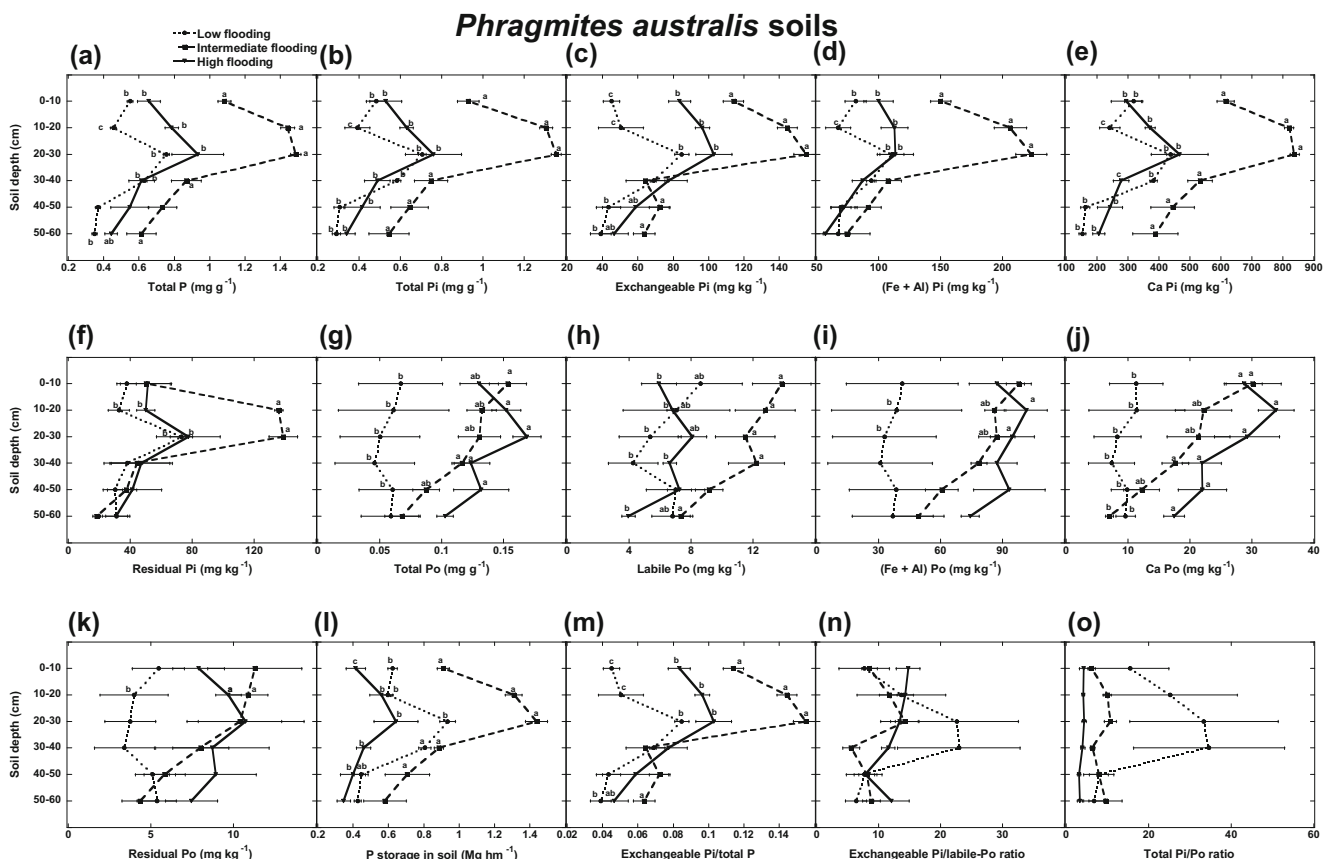


Fig. 9 Distribution of soil P variables (mean \pm SE, $n = 3$) in the soil profile of the wetlands dominated by *P. australis* subjected to low, intermediate, and high flooding intensities

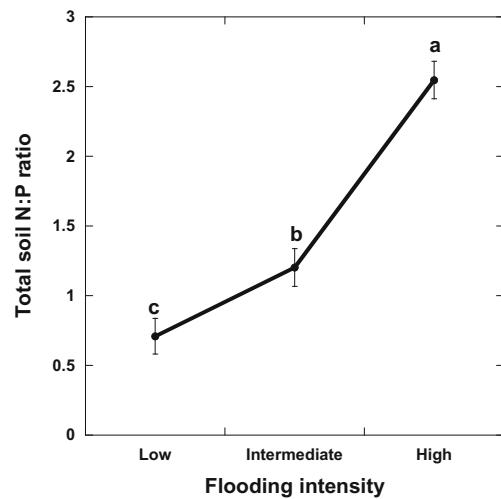
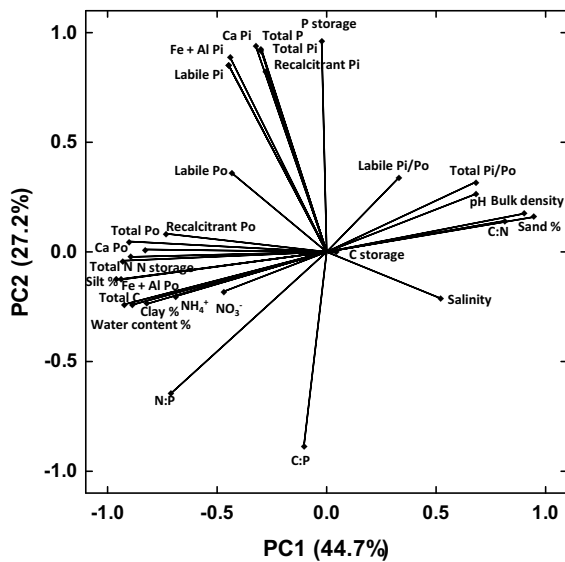


Fig. 11 Total N:P ratio (mean \pm SE, $n = 3$) in the soil profiles (0–60 cm) of the wetlands dominated by *P. australis* subjected to low and high flooding intensities

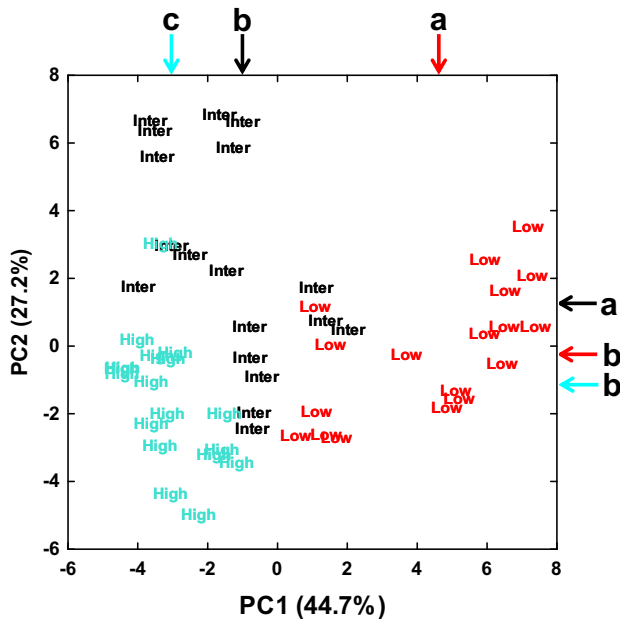


Fig. 10 Distribution of variables and cases in the plot of the first two PCs of the PCA analysis conducted with the P-fractions and other variables of the *P. australis* soils subjected to low, intermediate, and high flooding intensities. The arrows indicate the mean of the scores of *P. australis* wetland soils under different duration of flooding and different letters on arrows statistical significant differences ($P < 0.05$)

and 10.3 ± 0.12 , $P < 0.0001$, respectively) ratios. These results are consistent with some observed results regarding soil P. For example, the lower soil recalcitrant Po and higher labile Pi/Po ratio in soils under *P. australis* than in soils under *C. malaccensis* suggest higher decomposition rates of organic P consistent of litter with lower N:P ratio related with higher microbial growth rates and activity such as expected in the frame of ecological stoichiometry approach (Mooshammer et al. 2012; Zechmeister-Bolstenstern et al. 2015).

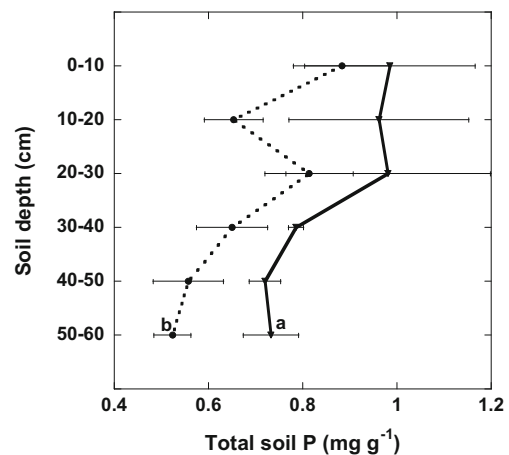
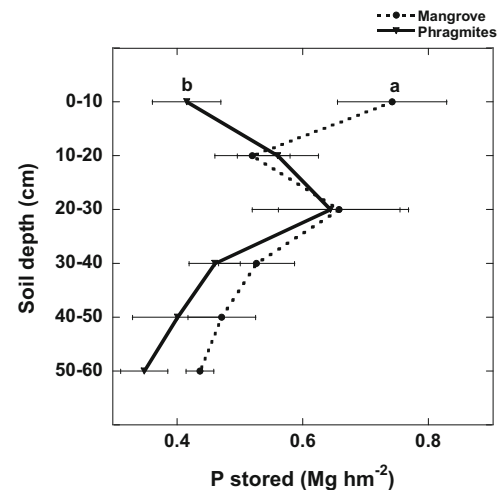


Fig. 12 Distribution of P stored in the soil and total soil P concentrations (mean \pm SE, $n = 3$) in the soil profiles of the wetlands dominated by *P. australis* and the native mangrove community subjected to high flooding intensity

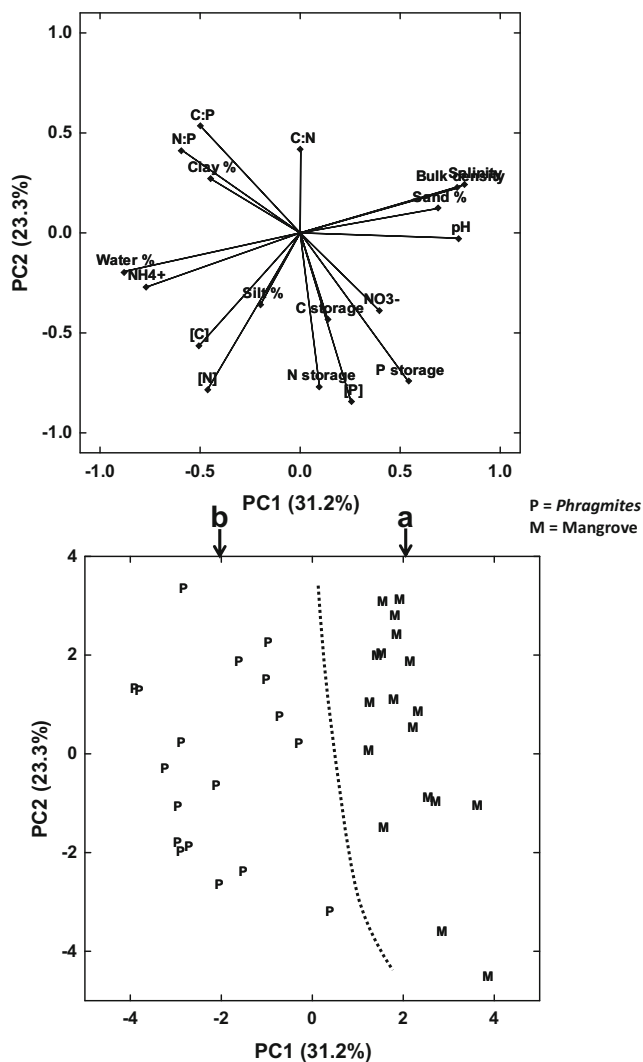


Fig. 13 Principal component analysis of the soil traits as variables and soil samples analyzed in experiment 3 (*P. australis* and mangrove wetland soils in an area of the Shanyutan wetland with high flooding intensity)

Differences Among Species of Flooding Effects on P Status

Concentrations in the Pi fractions in the upper 30 cm of the *P. australis* soils were higher at the highest flooding intensity than at the lowest and intermediate flooding intensities, whereas concentrations in the Po fractions were lowest at the lowest flooding intensity. The TP stored in soil and the exchangeable Pi:TP ratio in the upper 30 cm of soil were both highest at the intermediate flooding intensity. The intermediate flooding intensity thus produced the highest accumulation of P and the highest proportion of plant-available P in the *P. australis* soils. The biomass of the invasive *P. australis* was thus higher than those of *S. triquetra* and *C. malaccensis* ($P < 0.05$) in the high-flood habitat but was only higher than that of *S. triquetra* ($P < 0.05$) in the low-flood habitat (Wang et al. 2015b). The higher exchangeable Pi: labile Po ratio in the upper

30 cm of soil at the intermediate flooding intensity in the *P. australis* wetlands suggested that the mineralization rates would be higher at the intermediate flooding intensity, within the range tested in this study.

The N:P ratios in the *P. australis* soils increased with flooding intensity, as also observed when comparing the three species at two flooding intensities. A higher N:P ratio should mitigate the N limitation observed in other studies in this same wetland area (Wang et al. 2014). N:P ratios of 5.4–5.7 have been considered as indicating that a wetland is a P sink (Jimenez-Carceles and Alvarez-Rogel 2008). The range of the total N:P ratio (0.5–3) in this wetland area is thus very low, and N is also probably limiting at the highest flooding intensity. Our results thus also suggest that these wetlands are strong P sinks, with consequently low N:P ratios, and that the N:P ratio increases at higher flooding intensities with increases in N accumulation and not by decreases in P content. The capacity to store P at different flooding intensities is a key question in the estuarine wetlands of China, because cropland soils have very high P concentrations (MacDonald et al. 2011; Wang et al. 2014), consistent with the large amount of P stored in this estuarine area. This capacity to store P is even more crucial in the wetlands of subtropical China, where the high temperatures produce high rates of P mineralization (Rui et al. 2012) and the strong rains cause severe erosion in the river basins, which increase the transport of P from upriver to estuarine areas (Tian et al. 2010).

Our results thus suggest that the best management strategy for maximizing the capacity of this wetland area to act as a P sink should favor the combination of *C. malaccensis* and *P. australis* wetlands in areas of low flooding intensity ($<180 \text{ d y}^{-1}$ inundation) and the combination of *S. triquetra*, *C. malaccensis*, and *P. australis* wetlands in areas of intermediate-high flooding intensities ($>180 \text{ d y}^{-1}$ inundation).

Effects of Mangrove and *P. australis* Wetland on the Status of Soil P

In contrast with the previous results suggesting a closer positive relationship between clay content and the different P fractions, especially the Po fractions, the sandier soils in the mangrove community stored higher amounts of P in the upper 10 cm of soil than the less dense soil in the *P. australis* wetlands at similar flooding intensities. The higher soil density in the mangrove community allowed a higher total accumulation of P, despite the higher P concentration in the *P. australis* community. This capacity may thus be responsible for the large structural difference between these two communities. Mangrove ecosystems have a large capacity to retain soil nutrients (Tam and Wong 1996; Silva et al. 1998). The slow decomposition of wood in the upper soil layers could play a large role in this capacity (Romero et al. 2005). Nielsen and Andersen (2003) observed that P in the Bangrong mangrove

forest in Thailand tended to be concentrated in the leaf litter during decomposition, which was associated with the high P concentrations in the soils. These results suggest that the maintenance of native mangrove communities to act as P sinks is the best management strategy in wetland areas with high flooding intensities ($>220 \text{ d y}^{-1}$ inundation). Our results strongly suggest that the best management strategy that would both preserve biodiversity and maximize the capacity of the wetland area to act as a P sink for future scenarios of rise in flooding duration, should favor the combination of *C. malaccensis* and *P. australis* wetlands in areas with low flooding intensity ($<180 \text{ d y}^{-1}$ inundation), the combination of *S. triqueter*, *C. malaccensis*, and *P. australis* wetlands in areas with intermediate flooding intensity ($180\text{--}220 \text{ d y}^{-1}$ inundation), and the maintenance of native mangrove communities in areas with high flooding intensities ($>200 \text{ d y}^{-1}$ inundation). In fact, this wetland area has been recently declared as National Reserve and some of the current mangrove areas have been planted by China government. This study thus shows the positive results of this policy of repopulation of native mangrove communities in the higher flooded areas to rise the capacity to store P in soil and to avoid eutrophication.

Conclusions

Flooding moderately increased TP accumulation, P concentrations in several P fractions, and the exchangeable Pi:labile Po ratio. Some indirect effects of flooding, such as increases in soil salinity and total S concentrations, contributed to the moderation of the relationship between flooding and the P fractions by counteracting the direct positive relationship with flooding. This moderation occurred because these variables were negatively correlated with total P accumulation, P concentrations in several P fractions, and the exchangeable Pi:labile Po ratio.

We observed an interaction between species and flooding on the total-P and P-fraction concentrations. The relationship between flooding and higher P-fraction concentrations depended on the species community. The principal cause of this relationship was the relationship of each species with the increase in clay content as flooding increased. Clay content was the soil variable most positively correlated with the various P-fraction concentrations and was more dependent on the dominant species than on the flooding intensity alone.

Higher clay contents were correlated with higher S concentrations and lower pHs, consistent with the higher anoxic conditions expected in soils with higher clay contents. Clay content was also correlated with a higher adsorption capacity. All these soil conditions at high clay contents are consistent with lower Po availability to microorganisms and consequently with conditions unsuitable for mineralization and thus with

higher Pi concentrations and especially with higher Po concentrations (low Pi:Po ratio).

Thus, taking into account future scenarios of flooding intensity rise and the projected scenarios of the amounts of P received by coastal waters from rivers in China (Strokal et al. 2014), a suitable management to both preserve biodiversity and to maintain this wetland area in optimum conditions to act as a natural eutrophication buffer should tend to favor mangrove communities in the new areas that reach more than 220 days y^{-1} of flooding, and the combination of the three tall-grasses below this level of flooding.

Acknowledgments This work was supported by grants from the National Science Foundation of China (31000209), the Fujian Provincial Department of Education Foundation (JA13081), the European Research Council Synergy grant ERC-2013-SyG-610028 IMBAL-ANCE-P, the Spanish Government (CGL2013-48074-P) and the Catalan Government (SGR 2014-274).

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